

The University of Chicago

MORPHOLOGY AND ANATOMY OF
THE FRUIT OF HICORIA PECAN

A PART OF THE DISSERTATION SUBMITTED
TO THE GRADUATE FACULTY IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
DONALD VINCENT SHUHART

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MORPHOLOGY AND ANATOMY OF THE
FRUIT OF HICORIA PECAN

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DONALD V. SHUHART

(WITH FORTY-FIVE FIGURES)

I. Introduction

European investigators of the Juglandaceae have studied the morphology of *Juglans regia* chiefly, while in America *Hicoria pecan* has received most attention. A thoroughly critical investigation of the vascular anatomy of the fruit of *H. pecan* or of any other species of this family has not been recorded.

In 1862 DE CANDOLLE (5) concluded that the ovule of the Juglandaceae was orthotropous, sessile, and its placentation free central. He pointed out also that the cotyledons in this family were bifurcated. ROWLEE and HASTINGS (12) agreed with DE CANDOLLE on the interpretation of the cotyledons in several species of *Juglans* and *Hicoria*. VAN TIEGHEM (15) suggested that the ovule might be considered anatropous, and attempted an interpretation of its vascular system. BRAUN (4) concluded that the inner structure of the nut of *Juglans* and of *Hicoria* were the same. NAWASCHIN (9) reported chalazogamy in *J. regia*. He pointed out that winged evaginations developing from the placenta perpendicular to the septum were pressed against and fused with the walls of the ovary, serving as a medium through which the pollen tube passed on its way to the ovule. BILLINGS (3) reported chalazogamy in *H. pecan*, agreeing essentially with the report of NAWASCHIN. He illustrated the vascu-

lar system of the ovule as diverging at right angles from the septal bundles. KARSTEN (11) concluded that no megaspore mother cell was differentiated in the carpellate flowers of *Juglans* and *Hicoria*, but that a general sporogenous tissue gave rise to the megagametophyte. NICOLOFF (10) confirmed the work of DE CANDOLLE in all important features, including the free central placentation of the ovule of *J. regia*. He did not find the general sporogenous tissue described by KARSTEN, nor was he able to distinguish an archespore. N. C. WOODROOF (18) concluded that a megaspore mother cell gave rise to a linear tetrad of megaspores in *H. pecan*, and that the chalazal megaspore developed into the megagametophyte. BENSON and WELSFORD (2) attacked the view of NICOLOFF (10) concerning the mode of placentation and concluded that the notion presented by VAN TIEGHEM (15) was correct. These investigators described and illustrated diagrammatically the vascular system of *J. regia*, and concluded that the septal bundles represented the marginal bundles of the carpels. SHUHART (13) concluded that the primordia of the carpellate flower of *H. pecan* were initiated in the spring of the year in which they are pollinated, and traced early stages in the development of the fruit. WOODROOF and WOODROOF (16) agreed on the time of initiation of carpellate flower primordia, and later (17) called attention to the vascular bundles which are within the shell of *H. pecan*. They also traced later stages in the development of the embryo. ISBELL (8) confirmed former workers as to the time at which carpellate flowers of *H. pecan* were differentiated. ADRIANCE (1) recently called attention to the similarity in the orientation of the stigmas of *J. regia* and *H. pecan*. He concluded that the ovule of the latter was orthotropous and sessile, and illustrated a portion of the septal bundles.

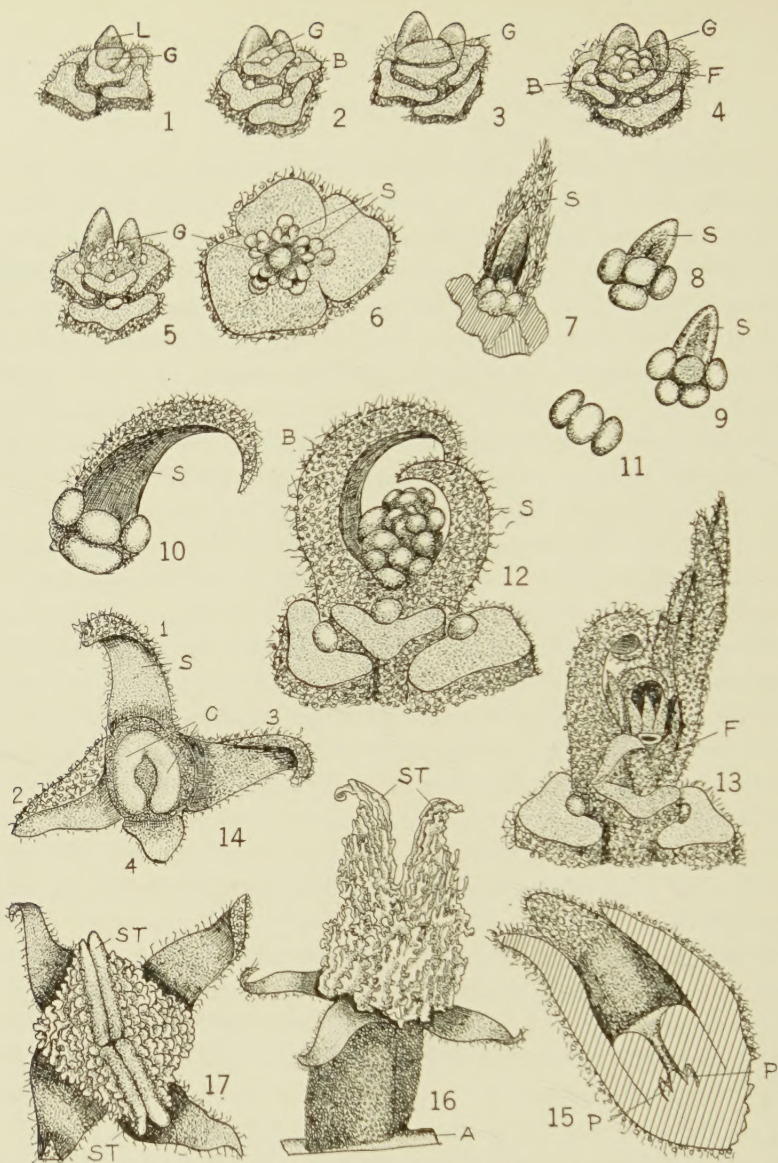
II. Bracts and sepals

The four-lobed calyx of the carpellate flower of *Hicoria pecan* persists in the mature fruit. Lines continuous with the edges of the four sepals are traceable on the cupule along the lines of its sutures. The outer sepal of some of the lower flowers of the cluster is greatly enlarged, and has been thought by some workers to represent a member undiverged from the subtending bract of the individual flower.

Several stages of development in the inflorescence precede the

initiation of the sepal primordia. Following the broadening of the growing point, described by SHUHART (14) as the first visible stage in the differentiation of the carpellate inflorescence in *Hicoria pecan*, the primordium for the entire floral axis appears in the center of this broadened area (figs. 1-3). There soon appears on the area surrounding this axial primordium a group of five lateral primordia, each of which eventually develops as an individual flower (figs. 4-6). Judging from the later appearance of the inflorescence, these primordia are spirally arranged in the same manner as the leaves of the stem, although they appear as a cycle early in their development. According to DE CANDOLLE (5), VAN TIEGHEM (15), and NICOLOFF (10), in other species of the Juglandaceae each of these lateral protuberances is the primordium of a bract subtending an individual flower; such is not the case in *Hicoria pecan*. In this species two of the upper leaf primordia usually develop into large bracts which fold over the other members of the developing floral cluster. One of the two or three serial bud primordia in the axil of each of these bracts sometimes develops into carpellate flowers. The outer sepals of such flowers are entirely separate from the bract (fig. 13). The other primordia, which fail to differentiate into carpellate flowers, are vegetative buds even though located on the peduncle of the inflorescence, this being the method of origin of the false terminal buds of type four referred to by SHUHART (14).

The protective function of the bracts which develop from the upper leaf primordia is augmented by the greatly enlarged outer sepal on the first or second flower of the cluster (figs. 7, 10, 12). Median flowers of the cluster do not develop such large outer sepals (figs. 8, 9). The upper flower primordia of the inflorescence sometimes fail to initiate more than two sepal primordia (fig. 11). This results in the occasional development of a flower with a two-lobed perianth. A critical study of the vascular system of the enlarged outer sepals of the lower flowers of several varieties of *Hicoria pecan* revealed no vestige of a structure corresponding to the bracts described by NICOLOFF (10) for *Juglans*. Bracts need not be present in the upper flowers since the habit of *H. pecan* is to develop several serial buds in the axil of a single leaf. If the bract is considered as present then it is undiverged from the flower.



FIGS. 1-17.—Fig. 1, last leaf primordia (*L*) and growing point (*G*) of dormant, subterminally lateral bud in November; no primordia of axillary buds present. Fig. 2, narrow growing point (*G*) of vegetative bud after growth has started in spring; axillary bud primordia (*B*) formed. Fig. 3, broadened growing point (*G*) of blossom bud just as growth is starting in spring but before axillary bud primordia have formed. Fig. 4, primordia of carpellate flowers (*F*) developed simultaneously with primordia of upper axillary buds (*B*); growing point (*G*) of axis of inflorescence at center of group of five flower primordia. Fig. 5, growing point of axis of inflorescence (*G*). Fig. 6, top view of fig. 5 showing sepal primordia (*S*). Fig. 7, lower flower of Schley variety showing greatly enlarged outer sepal (*S*). Fig. 8, median flower showing only slight enlargement of outer sepal (*S*). Fig. 9, median flower showing five sepal primordia. Fig. 10, lower flower of Indiana variety showing greatly enlarged outer sepal (*S*). Fig. 11, upper flower with only two sepal primordia (these sometimes develop into a 2-lobed perianth). Fig. 12, young inflorescence of Indiana variety; function of single bract (*B*) augmented by the greatly enlarged outer sepal (*S*) of first flower of cluster. Fig. 13, inflorescence of Schley variety showing carpellate flower (*F*) which developed from primordium in axil of last compound leaflet. Fig. 14, primordia of carpels (*C*) (laterally located with reference to axis of inflorescence). Fig. 15, two protuberances (*P*) lateral to placenta and in plane of septum observed in flower dissected under binocular. Fig. 16, carpellate flower of Schley variety; plane of stigma tips (*ST*) parallel to axis of inflorescence (*A*). Fig. 17, unnamed variety showing indication of bifurcation of stigmas to form stigma tips (*ST*) (cf. figs. 14 and 16); plane of stigma tips perpendicular to plane of dorsal bundles of carpels.

SHUHART (14) observed that in the Burkett variety four points on the apparently single primordium of the flower elongated more rapidly than the remaining portion, thus giving rise to the four-sepal primordia almost simultaneously. The order of sequence in the initiation of the sepals of this flower, when a difference in the time of initiation is noticeable, does not agree entirely with that found in *Juglans regia* by VAN TIEGHEM (15). The abaxial sepal primordium forms first; the two lateral primordia are then formed; and the adaxial sepal is the last member of the perianth to be initiated (fig. 14).

In their early development the sepals fold over and protect the inner parts of the flower. As floral development progresses they unfold so that at pollination time they extend laterally as four approximately equal, relatively thick, tapering divergences from the top of the receptacle (fig. 16).

III. Cupule

The cupule of *Hicoria pecan* comprises that portion of the fruit which dehisces from the nut at maturity. It is a specialized stem, and may be regarded as a cup-shaped receptacle dehiscing at four parenchymatous rays which are continuous with the edges of the sepals. In some varieties these sutures are extended outwardly into keel-shaped structures, while in others there is almost no external indication of the lines of dehiscence. Dehiscence occurs not only between the four sectors of the cupule, but also at the surface of the nut.

Transverse sections of a young fruit show a line of thin-walled parenchyma surrounding that portion of the carpel wall which matures as a shell. This parenchyma is continuous with the similar parenchyma of the sutures between the four sectors of the cupule. Each sector of these sections contains a segment of an outer ring of bundles. Each segment of this ring is made up of from 15 to 20 collateral bundles which are completely ensheathed in parenchyma, and which show normal orientation. In addition to this outer ring there is an inner ring of a smaller number of bundles (figs. 22-26). The inner ring of bundles is adjacent to the thin-walled parenchyma which is the line of dehiscence between the cupule and the shell of the nut. The collateral bundles of the inner ring are likewise ensheathed in parenchyma, but they show reversed orientation.

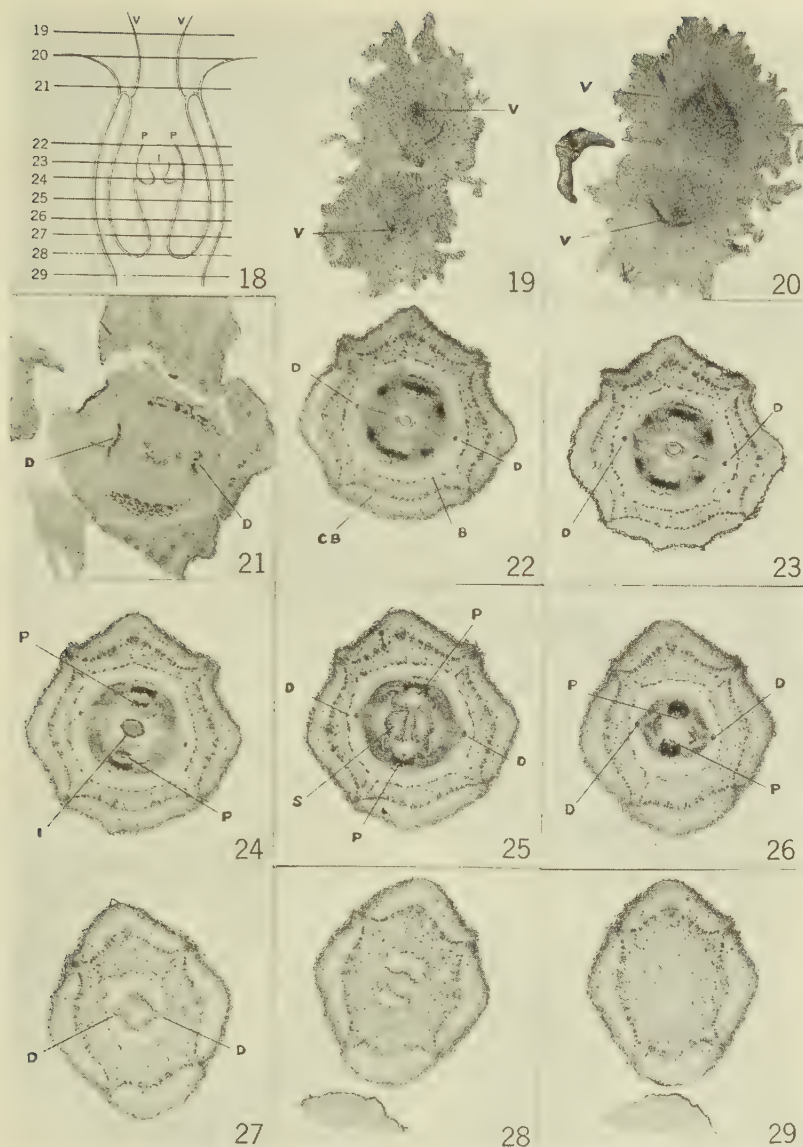
Radial sections through a mature flower show that the bundles of the outer ring as seen in transverse section are extended to a level just below the top of the cupule, thus forming an outer vascular cylinder dissected by four parenchymatous rays. At the top of this cylinder the sepal bundles diverge. The cylinder of bundles then extends inward for a short distance, and then downward, resulting in complete reversal of the orientation of the bundles. This reversal occurs at lower levels along the lines of dehiscence of the cupule, but the majority occurs in the upper portion. These reversely oriented bundles extend to the base of the cupule, thus forming an inner cylinder of reversely oriented bundles. In both abaxial and adaxial sectors of the cupule, some vascular bundles diverge from the inner cylinder of bundles at a level slightly below the top of the cylinder (figs. 18, 19, 20, 42). These bundles extend to the tips of the stigmas. No divergences corresponding to these occur in the two lateral sectors.

The area between the outer cylinder of bundles and the outside of the cupule consists of cortical parenchyma and an epidermal layer of cells from which arise many glandular hairs. This tissue is an extension of the cortex of the stem. The area between the outer and inner ring of bundles is an extension of the medullary parenchyma of the stem. In both the cortical and the medullary parenchyma of the stem many cells are filled with a densely staining substance, and many contain crystals of calcium oxalate. These same substances are present in the cortical and medullary parenchyma of the cupule.

At the base of the cup-shaped receptacle, the inner cylinder of reversely oriented bundles again extends toward the center and is again extended upward so that it forms a third cylinder of bundles at this level (fig. 27). It is at this point that the dorsal bundles of the carpels diverge.

IV. Carpels

In *Hicoria pecan* the two carpels which normally form the ovary are lateral with respect to the axis of the inflorescence, and are occasionally distinguishable from each other at the time of their initiation by a slight indentation between the carpels (fig. 14). Often these indentations are entirely absent, and the carpels appear to develop as an unbroken ridge of tissues around the retarded central part of the axis. The carpels continue to develop, forming a tubular



FIGS. 18-29.—Fig. 18, diagram of vascular system of *H. pecan* through septal bundles showing location of cross-sections shown in figs. 19-29. Fig. 19, vascular bundles (V) which diverge from stele at top of cupule and extend to stigma tips. Fig. 20, same vascular bundles (V) at lower level; dorsal bundles absent. Fig. 21, at point of divergence of sepals; dorsal bundles (D) extend slightly above this level. Fig. 22, outer (CB) and inner (B) rings of cupule bundles; dark areas are groups of parenchyma cells filled with deeply staining substance, probably tannin. Fig. 23, median section through ovule. Fig. 24, septal bundles (P) and bundles of integument (I) (note typical stelar cylinder which these latter bundles form). Fig. 25, two groups (S) of horizontally extended bundles in center of septum which are continuous with septal bundles (P) at higher level (note the two slitlike locules). Fig. 26, second septum beginning to form at base of the two locules. Fig. 27, showing three stelar rings, all of which are the same bundles differently oriented: outer ring is normally oriented; middle ring is reversely oriented; and center ring is also normally oriented; dorsal bundles (D) diverging from stele. Fig. 28, showing point at which upward extension of second ring of bundles occurs. Fig. 29, showing absence of connections between bundles of inner rings and those of outer ring below carpels (and very few occur below the level of base of ovule).

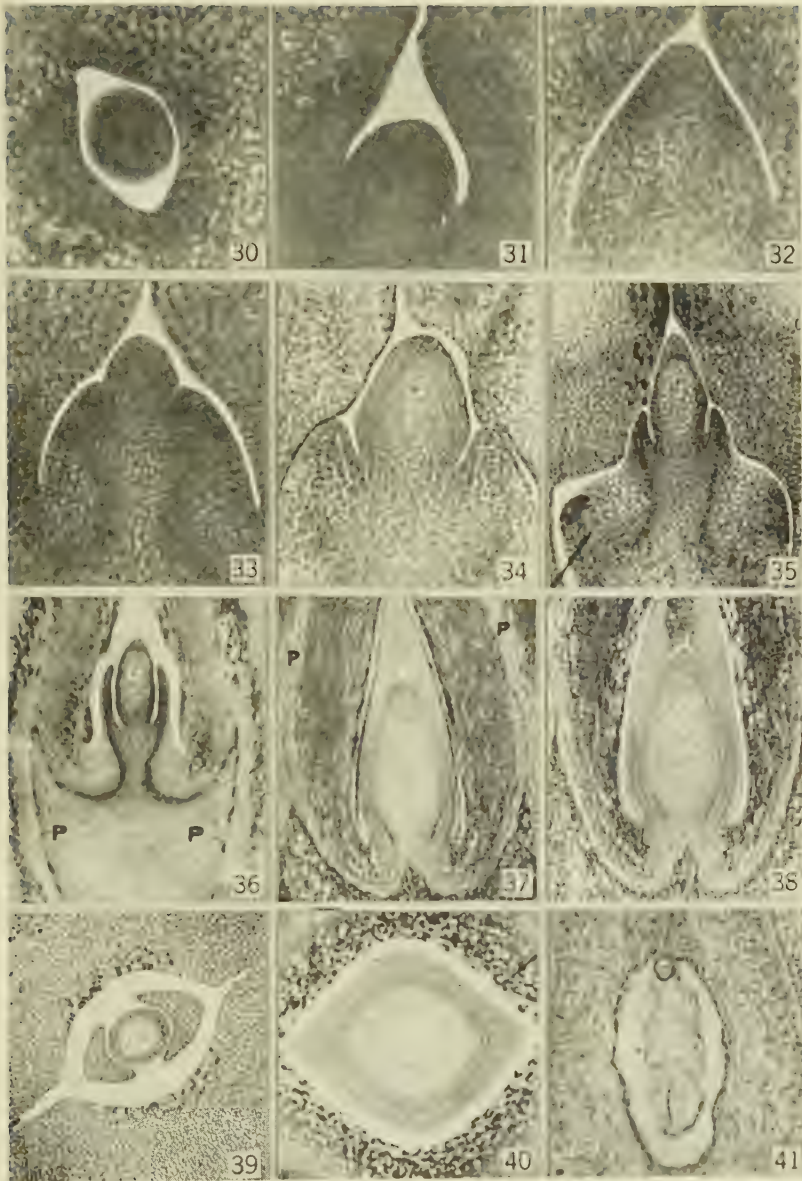
structure; the axis elongates independently of and free from them. When the carpels are approximately 1 mm. in length, the growing point of the axis has formed a columnar central placenta.

The exact manner in which the septum is developed has proved difficult to ascertain. Some evidence exists which apparently indicates that two protuberances, on opposite sides of the central columnar placenta and in the plane between the two carpels, grow against and actually fuse with the inner edges of the carpels.

DE CANDOLLE (5) pointed out that the ovaries in the Juglandaceae are at first uniloculate with a centrally elevated columnar placenta. NAWASCHIN (9) stated that this central placenta was not elevated freely but was in contact with the walls of the ovary and even fused with it in certain places. NICOLOFF (10) agreed that the placenta was not columnar in form. In *Hicoria pecan* the free columnar nature of the placenta is observable for only a very few days following its initiation (figs. 30, 31). Soon the initiation of the nucellus and the integument, together with the elevation of two areas or ridges, extending abaxially and adaxially with respect to the axis of the inflorescence, more or less completely hides its early columnar nature. Further growth of the carpels results in the development of two large stigmas which often have deep, tortuous, forking, and intersecting folds.

DE CANDOLLE (5) pointed out that the mid-plane of the stigmas of *Juglans* is parallel to the axis of the inflorescence, while that of *Hicoria* is transverse to this axis, thus corresponding to the arrangement of the carpels. ADRIANCE (11) called attention to the fact that the plane of the stigmas was the same in both *J. regia* and *H. pecan*. A study of this point confirmed the observation of ADRIANCE, and further revealed that each stigma tip in *H. pecan* is apparently bifurcated. In the normal two-carpelled flower, each tip of one carpel resulting from such bifurcation is undiverged from the adjacent tip of the opposite carpel (figs. 16, 17).

The vascular system of the carpels consists of either two or three sets of bundles, depending on the manner in which it is interpreted. A transverse section at the base of the ovule shows two dorsal and two septal bundles. The septal bundles extend slightly above the top of the ovule. These two pairs of bundles originate from the third



FIGS. 30-41.—Fig. 30, columnar placenta. Fig. 31, longitudinal section of columnar placenta. Fig. 32, primordium of ovule on columnar placenta. Fig. 33, primordia of nucellus and integument. Fig. 34, ovule at archesporial stage. Fig. 35, ovule at linear tetrad stage. Fig. 36, ovule at 8-nucleate stage of megagametophyte. Fig. 37, ovule with long integument after fertilization. Fig. 38, ovule with short integument after fertilization. Fig. 39, transverse section near tip of integument showing its bifurcation. Fig. 40, transverse section of ovule after fertilization, showing endosperm. Fig. 41, zygote and endosperm.

ring of bundles referred to in the discussion of the cupule. A transverse section through the stigmas at a low level shows the two dorsal bundles and two bundle groups which are in the same plane as the septal bundles (figs. 21, 24). These latter are those bundles which extend to the tips of the stigmas. They diverge from the inner cylinder of the bundles of the cupule and are therefore reversely oriented at the level at which they diverge. They soon extend toward the tips of the stigmas and are normally oriented.

WOODROOF and WOODROOF (17) indicated the presence of two vascular bundles in the shell and also two in the septum of *Hicoria pecan*. VAN TIEGHEM (15) as well as BENSON and WELSFORD (2) pointed out that the dorsal bundles of *Juglans regia* are not included in that portion of the ovary which becomes the shell of the nut. These investigators considered the septal bundles as representing the lateral bundles of the inturned edges of the carpels. In *J. regia* they did not find bundle groups similar to those which extend to the tips of the stigmas in *H. pecan*. The writer has observed that the main bundles which extend to the tips of the stigmas in *J. regia* are the dorsal bundles of the carpels, but they appear to have other bundles associated with them. These latter bundles, however, are not the extended septal bundles as VAN TIEGHEM (15) thought. In *H. pecan* the dorsal bundles of the carpels extend approximately to the point at which the apparent bifurcation of the stigmas occurs. If the septal bundles are considered as the marginal bundles of the inturned edges of the carpels, this part of the vascular system corresponds to the dorsal and placental bundle complex frequently found in carpels; but those bundles which extend to the tips of the stigmas in *Hicoria pecan* are entirely disregarded.

Some evidence has been observed which suggests that the septal bundles may be axial in nature. If this be true, another possible interpretation of the vascular system is to consider the bundles which extend to the tips of the stigmas as the marginal bundles of the carpels, designating as dorsal bundles the same bundles as in the former case, and then considering the axial placenta as growing conjointly with the edges of the carpels on the adaxial-abaxial sides, just as it does in the opposite plane when a second septum is formed, thus producing a septum which is chiefly axial in nature.

The apparent protuberances which seem to diverge from the axis and which appear to grow against and fuse with the carpel walls may contain those provascular strands which in later development result in the septal bundles extending to a level above the top of the ovule. The apparent initiation of the protuberances occurs at a point so near the base of the carpels that they involve all of the base of the uniloculate ovarian cavity on the two sides where they occur. This seems to result in the very rapid change from a uniloculate to a biloculate condition of the lower part of the cavity. At the point at which these protuberances seem to be initiated, the columnar placenta is so completely meristematic that no well differentiated epidermis exists. No line of epidermis has been found after the apparent fusion has taken place. This fact has limited the evidence in support of this view to the apparent protuberances on the columnar placenta immediately before the formation of the septum, and to the fact that in the dissection of a flower soon after formation of the septum began two well developed lateral protuberances have been observed (fig. 15). These lateral protuberances are not to be confused with the "winged evagination" of NAWASCHIN (9), which are the "outer integument" of KARSTEN (11), the "horns" of NICOLOFF (10), and the "con crescent trichomes" of BENSON and WELSFORD (2). These variously named structures are not so conspicuous in *Hicoria pecan*, which has only a vestige of a second septum. In other members of the Juglandaceae, especially in *Juglans regia*, they appear to be an upward extension, above the base of the ovarian aperture, of that tissue which forms a second septum and are thus located in a plane at right angles to the plane of the original septum.

In his interpretation of the vascular system of the septum of *Juglans regia*, VAN TIEGHEM (15) concluded that after the divergence of all other bundles in the carpellate flower, four remaining bundles of the stele extended first toward the center and then upward, to form the placental bundles. He considered the dual vascular supply from these bundles to the ovule as equivalent to funiculi. BENSON and WELSFORD (2) agreed with these conclusions, and described the septal bundles as diverging from the stele at a higher level than that at which the dorsal bundles diverge.

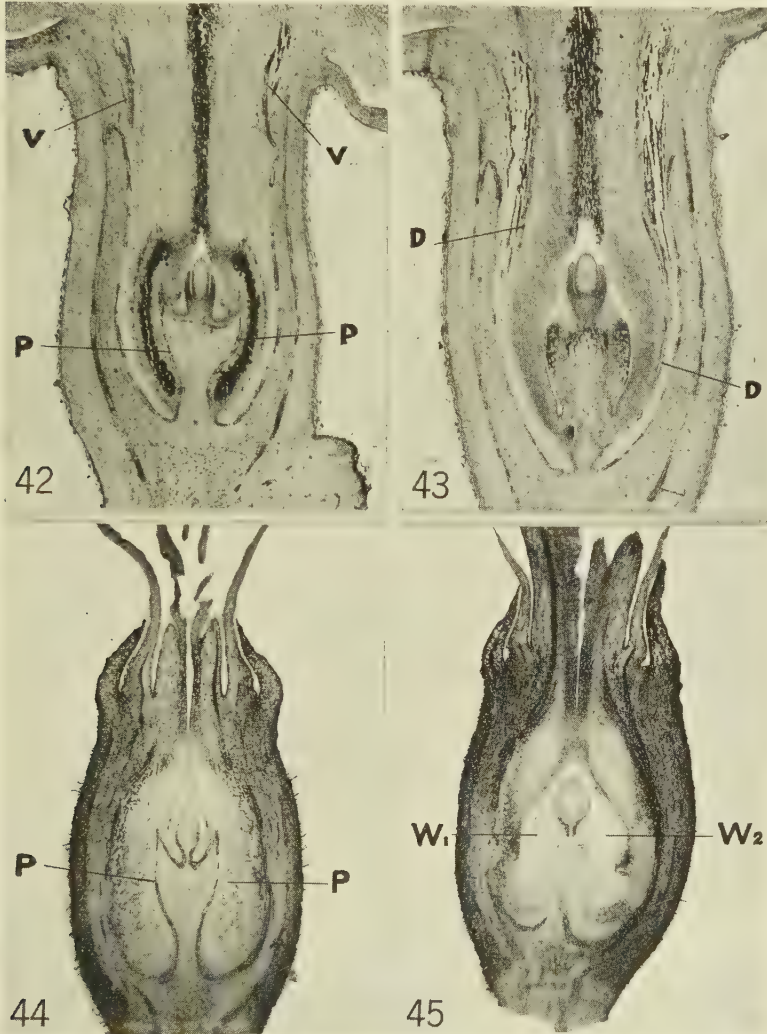
Observations made on *Juglans regia* by the writer did not entirely

agree with the findings of VAN TIEGHEM and BENSON and WELSFORD. The two septal bundles originate in exactly the same manner as they do in *Hicoria pecan*. This point, however, is very obscure in the former case (figs. 44, 45), whereas in the latter (figs. 42, 43) it is relatively easy to observe. Instead of three separate rings of bundles, as seen in a transverse section at the base of the cupule of *H. pecan*, a similar section of *J. regia* shows that the bundles are dispersed and present the appearance of a meristele. This condition persists more or less to about the level of the base of the ovule. Close observation of a section about the base of the ovule reveals that some of the inner bundles are either distinctly reversed in their orientation or appear as bicollateral bundles. Often only a single row of parenchyma cells separates the normally oriented bundle from the reversely oriented one. These reversely oriented bundles first extend to the proximal portion of the cupule and then extend inward almost to the center, just as they do in *H. pecan* (figs. 42-45). In *J. regia* the dorsal bundles diverge from those bundles of the stele which have been only normally oriented, while in *H. pecan* the dorsal bundles diverge from the third ring of bundles which are reversely oriented in the second ring. The septal bundles in *H. pecan* result from the anastomoses of those bundles which extend downward, then inward, and then upward near the center of the axis.

NICOLOFF (10) endeavored to explain the development of the ridges and cavities of the shell by stating that four regions at the base of the ovary and four regions in the upper portion become cavities by the arrest of growth. BENSON and WELSFORD (2) indicated the presence of a packing tissue, but did not explain its morphological significance. WOODROOF and WOODROOF (17) adopted this same term and mentioned that this material is pressed back against the shell of the nut. The intimation in each case is that cavities are first formed and are then filled with the packing tissue.

The inner tissue of the ovary, through differential development, forms a very thin-walled parenchymatous endocarp which assumes the contours in its development that the mature kernel of the nut will eventually have. Two cavities are formed by the arrest of growth at the base of the ovary, but these cavities do not assume the form of the mature kernel: they are present as narrow slits only.

The upper part of the ovarian cavity remains uniloculate, but four areas of parenchymatous endocarp develop in this region. The walls of this cavity are relatively smooth. The expansion of the integu-



FIGS. 42-45.—Fig. 42, radial section through septal bundles (*P*) of *H. pecan*. Fig. 43, radial section through dorsal bundles (*D*) of *H. pecan*. Fig. 44, radial section through septal bundles (*P*) of *J. regia*. Fig. 45, radial section through dorsal bundles of *J. regia* (the “winged evaginations” of NAWASCHIN (9) are present at *W*₁ and *W*₂).

ment due to the increased growth of the endosperm crushes this thin-walled parenchyma and thus it takes that form which was determined by the differential development of the carpellary tissue.

DE CANDOLLE (5) concluded that the ovary wall became the shell of the nut in the Juglandaceae. NICOLOFF (10) agreed with this interpretation, but neither of these workers mentioned the fact, pointed out by VAN TIEGHEM (15) as well as by BENSON and WELSFORD (2), that the dorsal bundles are not included in that portion which becomes the shell of the nut. While the mere differentiation of tissue due to lignification is not of sufficient morphological significance to distinguish that part which is carpel from that which is receptacle, the fact that the dorsal bundles are not included in the shell indicates that the shell of *Juglans regia* may be only a part of the ovary wall. In *Hicoria pecan*, however, these bundles are included in that portion which becomes the shell. Furthermore, the dried stigma often persists until maturity of the nut, and may be found on the end of a lignified style which connects it with the nut, thus indicating that the shell is the lignified outer portion of the ovary. Transverse sections of young nuts also substantiate this conclusion.

V. Ovule

The ovule of the Juglandaceae has been studied by DE CANDOLLE (5), VAN TIEGHEM (15), NAWASCHIN (9), KARSTEN (11), BILLINGS (3), BENSON and WELSFORD (2), N. C. WOODROOF (18), and ADRIANCE (1). These investigators, with the exception of BILLINGS, WOODROOF, and ADRIANCE, who studied *Hicoria pecan* only, limited their studies principally to *Juglans*. The development of the megagametophyte of the ovule of *H. pecan* has been studied critically by WOODROOF (18) alone. Each investigator, with the exception of VAN TIEGHEM (15) and BENSON and WELSFORD (2), has either concluded or accepted the opinions of others that the ovule is orthotropous, sessile, and axial. These three investigators cited an unusual case in which the vascular system of the ovule was present on one side only, and concluded that the ovule of the Juglandaceae is in reality anatropous, and that the usual case in which the vascular system is present on both sides is a derived form. EAMES and MACDANIELS (6) also illustrate this special case.

VAN TIEGHEM (15) also advanced the idea that the ovule of *Juglans* is formed from a single lobe of the carpellary leaf, and that the vascular bundles which supply the ovule are equivalent to funiculi. His view, however, was opposed at once by GERMAIN (7), who stated that in the majority of plants the ovule originates as a bud produced from a small mass of cellular tissue on the edge of a carpellary leaf.

The nucellus of the ovule in *Hicoria pecan* is initiated as a relatively narrow, bluntly conical primordium, terminating the short columnar placenta (fig. 32). It is a central prolongation of the axis. Within three days from the time of the appearance of this primordium, the integument is initiated at two points on opposite sides of the nucellus (fig. 33). The provascular strands of the ovule appear as downward, then inward, and then upward extensions of both septal bundles (fig. 36).

The initiation of the integument at two points in *Juglans* induced BENSON and WELSFORD (2) to state that the integument is dual in nature. The integument of *Hicoria pecan* is bifurcated at its upper end as a probable result of its initiation at two points, but no further indication of a dual integument exists (fig. 39).

The integument as a whole remains meristematic for a long time, making eventual expansion into all cavities within the shell possible. BILLINGS (3) concluded that the integument tightly inclosed the nucellus at the time of pollination. WOODROOF (18) observed that the integument only half inclosed the nucellus at the time of pollination, but mentioned that this might vary with varieties. She also noted that the time of pollination was simultaneous with the differentiation of the linear tetrad of megaspores. The time of pollination varies greatly with seasonal conditions, and to some extent with varieties. Usually it coincides with the differentiation of the eight nuclei of the megagametophyte (fig. 36). At this time the integument may be from one-half to two-thirds the length of the nucellus, which is not entirely inclosed until after fertilization. Sufficient variation exists to prevent the attachment of any morphological significance to the rate of development of the integument, as compared with that of the nucellus, unless there may be some bearing on chalazogamy (figs. 37, 38).

VI. Megagametophyte

While neither KARSTEN (11) nor NICOLOFF (10) was able to find a definitely differentiated megaspore mother cell in the species of Juglandaceae which they studied, WOODROOF (18) reported its presence in *Hicoria pecan*. This conclusion is confirmed by the present investigation. A well differentiated megaspore mother cell, the large nucleus of which has a very large nucleolus, was found in the nucellus of ovules approximately three days after the primordium of the nucellus was initiated (fig. 34). About three days later the four megaspores were present in a linear tetrad, and in approximately three more days three of the megaspores were disintegrating, while the fourth, or chalazal megaspore, was considerably enlarged (fig. 35). Six days later the eight nucleate megagametophytes were found (fig. 36). Fusion of the polar nuclei occurred soon after formation of the eight nuclei. This also confirms WOODROOF'S (18) conclusions.

VII. Endosperm and embryo

Fertilization occurred within two weeks after the maturity of the megagametophyte. Long delayed fertilization was not observed. The zygote lies at the micropylar end of the embryo sac (fig. 41). The nuclei of the endosperm apparently divide freely, as described by N. C. WOODROOF, migrating to the periphery of the embryo sac, where they are held together by a mass of protoplasm, forming a saclike structure which is apparently free of cell walls at first (figs. 40, 41). Later in its development cell walls are present. At the time the embryo begins to develop (about September 1 at Stillwater, Oklahoma), the cell walls of the endosperm appear as a network with a more or less hexagonal mesh when observed in tangential section. The inner portion of this saclike structure is occupied by a large vacuole filled with a clear fluid which gives an acid reaction and strongly reduces Fehling's solution. The endosperm digests the nucellus, and continues to increase in volume by frequent nuclear divisions and an increase of the central substance of its vacuole. The increasing volume apparently forces the enlarging integument first into the cavities of the carpels, and then results in the crushing and digestion of the very thin-walled parenchymatous endocarp. In this

way the integument takes the shape determined by the differential growth of carpellary tissue.

The development of the embryo has been observed to occur as described by WOODROOF and WOODROOF, except that orientation of the cotyledons of the embryo is opposite to that described by these workers. The plane of the cotyledons coincides with the plane of the middle septum. The cotyledons are bifurcated early in their development, and the halves of each cotyledon grow into each cavity as described by DE CANDOLLE (5), ROWLEE and HASTINGS (12), NICOLOFF (10), and others. The cotyledons of the embryo grow between the integument and the endosperm, digesting the latter as they grow, but eventually completely surrounding the endosperm before it is entirely digested. This results in much-folded cotyledons. At maturity these folds are tightly pressed together and are held in place by the integument. The remnant of endosperm between the folds consists of the thin crushed walls which persist after their contents have been digested by the embryo. This remnant of endosperm is apparently that tissue which has been referred to by WOODROOF and WOODROOF (17) as a membrane of unknown origin. In some varieties and under some cultural conditions the space between the folds of the cotyledons persists and appears as a cavity in the center of the kernels. In those nuts in which the folds of the cotyledons have been tightly pressed together, the only indication of their previous separation is the presence of a double line of epidermis where the two parts meet.

VIII. Summary and conclusions

1. The primordia of carpellate flowers, although spirally arranged, at first appear as a cycle of five protuberances on the broadened growing point of the axis. Bracts present at the base of the inflorescence sometimes have carpellate flowers in their axils. No vestige of a bract, either external or internal, could be distinguished as a part of the enlarged outer sepals of any of the flowers of the cluster.

2. The cupule of *Hicoria pecan* is a specialized stem and may be regarded as a cup-shaped receptacle of four sectors. Its vascular system as seen in transverse section consists of four segments of tissue, in which can be discerned an outer and an inner ring of bundles, dis-

sected into four groups by parenchymatous rays. The outer ring is a section of an outer vascular cylinder which is normally oriented, and from it the sepal bundles diverge near the top of the cupule. The bundles of the outer cylinder extend inward and then downward, so that an inner cylinder of bundles is formed. These bundles extend to the base of the cupule where they are directed upward again, so that a third cylinder is formed in the basal portion of the cupule. Two bundle groups diverge from the reversed bundles near the top of two of the sectors and are continued to the tips of the stigmas.

3. In *Hicoria pecan* the plane between the carpels, the plane of the stigmas, and the plane of the septal bundles coincide and are parallel to the axis of the inflorescence. In *Juglans regia* the plane of the stigmas is perpendicular to the plane of the septal bundles and the plane between the carpels. The two latter planes coincide and are transverse to the axis of the inflorescence. The stigma tips of *Hicoria pecan* apparently represent the undiverged halves of two bifurcated stigmas. The dorsal bundles of the carpels of *Hicoria pecan* diverge from the third ring of bundles. The remaining bundles of this ring form the septal bundles. The carpellary cavity, at first uniloculate, becomes biloculate in the lower portion by the conjoint growth of the axis and the septum. The shell of the nut is principally that portion of the carpel walls which matures as a hard lignified exocarp. The ridges on the inner surface are formed by the hardening of a mesocarp resulting from the differential development of carpellary tissue. The parenchymatous endocarp is pressed back and absorbed by the expanding integument.

4. The ovule is orthotropous, sessile, and axial in its dependence. The single integument is initiated at two points and remains bifurcated at its tip. A megaspore mother cell is observable approximately six days after the initiation of the primordium of the ovule. The chalazal megaspore continues to develop while the other three disintegrate. Fusion of the polar nuclei occurs soon after formation of the eight-nucleate stage.

5. Fertilization occurs approximately two weeks after pollination. The endosperm nuclei divide frequently and are arranged peripherally, forming a saclike structure, apparently free of cell walls. The

zygote lies at the micropylar end of the embryo sac and remains inactive for several weeks.

6. The cotyledons of the embryo are oriented transversely to the septum and are bifurcated at the edge of the septum. They are much folded and sometimes cavities are formed between the folds. In closely folded cotyledons the line of contact of the two parts is marked only by a double row of epidermal cells.

7. The fruit of *Hicoria pecan* is a kind of pome fruit and consists of a specialized stem which surrounds a normally two-carpelled but single-ovuled ovary. It matures dry, and dehisces along four parenchymatous rays and at the surface of the carpels. It includes the true fruit, which is a nut formed by the lignification of the exocarp into a hard shell surrounding a single, loose, two-lobed orthotropous seed, the embryo of which has bifurcated and folded cotyledons.

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OKLAHOMA A. & M. COLLEGE
STILLWATER, OKLA.

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